

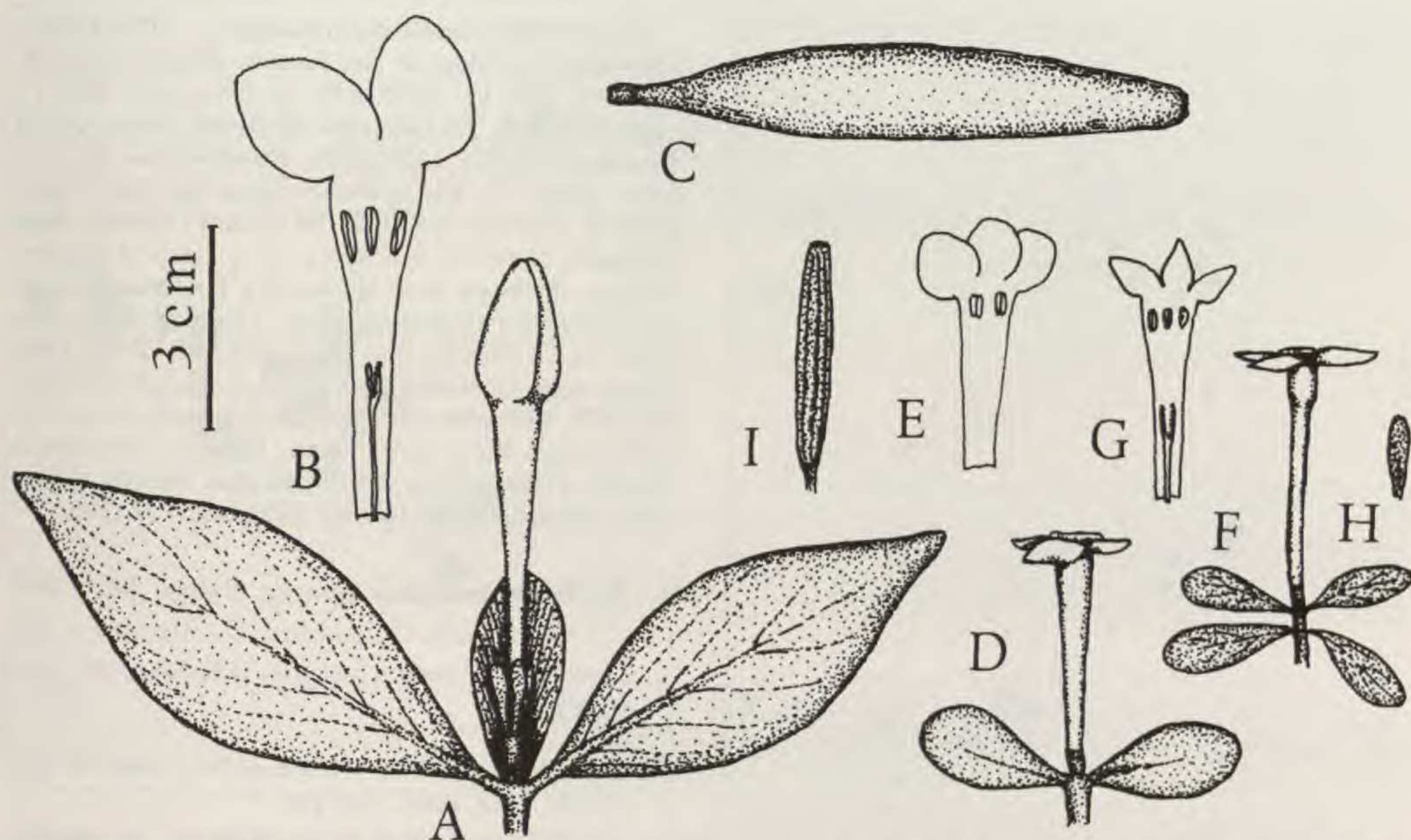


FIGURE 11. A-C. *Hillia loranthoides* Standl.—A. Habit with flower.—B. Flower opened.—C. Capsule. D, E. *Hillia palmana* Standl.—D. Habit with flower.—E. Corolla opened. F-I. *Hillia panamensis* Standl.—F. Habit with flower.—G. Flower opened.—H. Stipule (floral).—I. Capsule. A, from *Breedlove* 57488 (F); B, from *Brenes* 3839 (F); C, from *Williams* 41950 (F); D, E, from *Wilbur* 19782 (F); F, G, H, from *Dressler* 1487 (NY). A-G to same scale, H to twice this scale.

8. ***Hillia loranthoides*** Standley, J. Wash. Acad. Sci. 18: 165. 1928. TYPE: Costa Rica. Guana- caste: Quebrada Serena SE of Tilarán, ca. 700 m, 27 Jan. 1926, *P. C. Standley & J. Valerio* 46152 (holotype, US, photo F).

Hillia macrocarpa Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 23. 1943. TYPE: Guatemala. Quezaltenango: lower S-facing slopes of Volcán Santa María between Santa María de Jesús and Calajuache, along great barranca between Finca Pirineos and San Juan Patzulín, 1300–1500 m, 6 Jan. 1940, *J. A. Steyermark* 33667 (holotype, F, photo F).

Suffrutescent herbs or shrubs to 1.5 m tall; bark gray-brown, smooth. Leaf blades elliptic to somewhat oblanceolate, 2–10 cm long, 1.6–4.5 cm wide, acute to sometimes acuminate at apex with tip 3–5 mm long, cuneate to attenuate at base, coriaceous and usually thickly so; secondary veins pinnate, 3–5 pairs, plane, without domatia; margins flat; petioles 5–15 mm long; stipules 15–34 mm long, 8–14 mm wide. Flowers solitary; peduncles 1–4 mm long; bracts lacking or 1–3 × 1–2 mm; calyx limb lacking or divided to base, the lobes 4, 5–10 mm long, 1–4 mm wide, ligulate to oblanceolate, acute; corolla salverform, white, the tube 45–75 mm long, the lobes 4, 15–25 mm long, 10–24 mm wide, elliptic, rounded; anthers

4, 7–8 mm long, subsessile, with tips positioned 5–8 mm below top of corolla tube; ovary 3–10 mm long; styles 13–15 mm long; stigmas 8–12 mm long, linear, positioned below middle of corolla tube. Capsules 30–75 mm long including a beak 1–3 mm long, 5–11 mm diam., without stipes, smooth; seeds 1.5–4 × ca. 0.5–1 mm, with filaments 6–13 mm long. Figure 11A–C.

Habitat, phenology, and distribution (Fig. 12). Southern Mexico to northern Guatemala and northern to central Costa Rica, in wet forests at 700–2700 m. Collected in flower December to June, in fruit in January, March, and May.

This species differs from *Hillia tetrandra* and *H. maxonii* in its acute or shortly acuminate, usually very thickly coriaceous leaf blades. It may represent an acute-leaved variant of *H. maxonii*. Aside from geographic range, no features separate the plants of Mexico and Guatemala described as *H. macrocarpa* from those of Costa Rica, and this name is placed in synonymy here. The resultant apparently disjunct range of this species is similar to that of *H. panamensis* and some species of *Psychotria* (Hamilton, 1989). The report of *H. triflora* from southern Mexico (Taylor, 1989) was a misidentification of *H. loranthoides*.

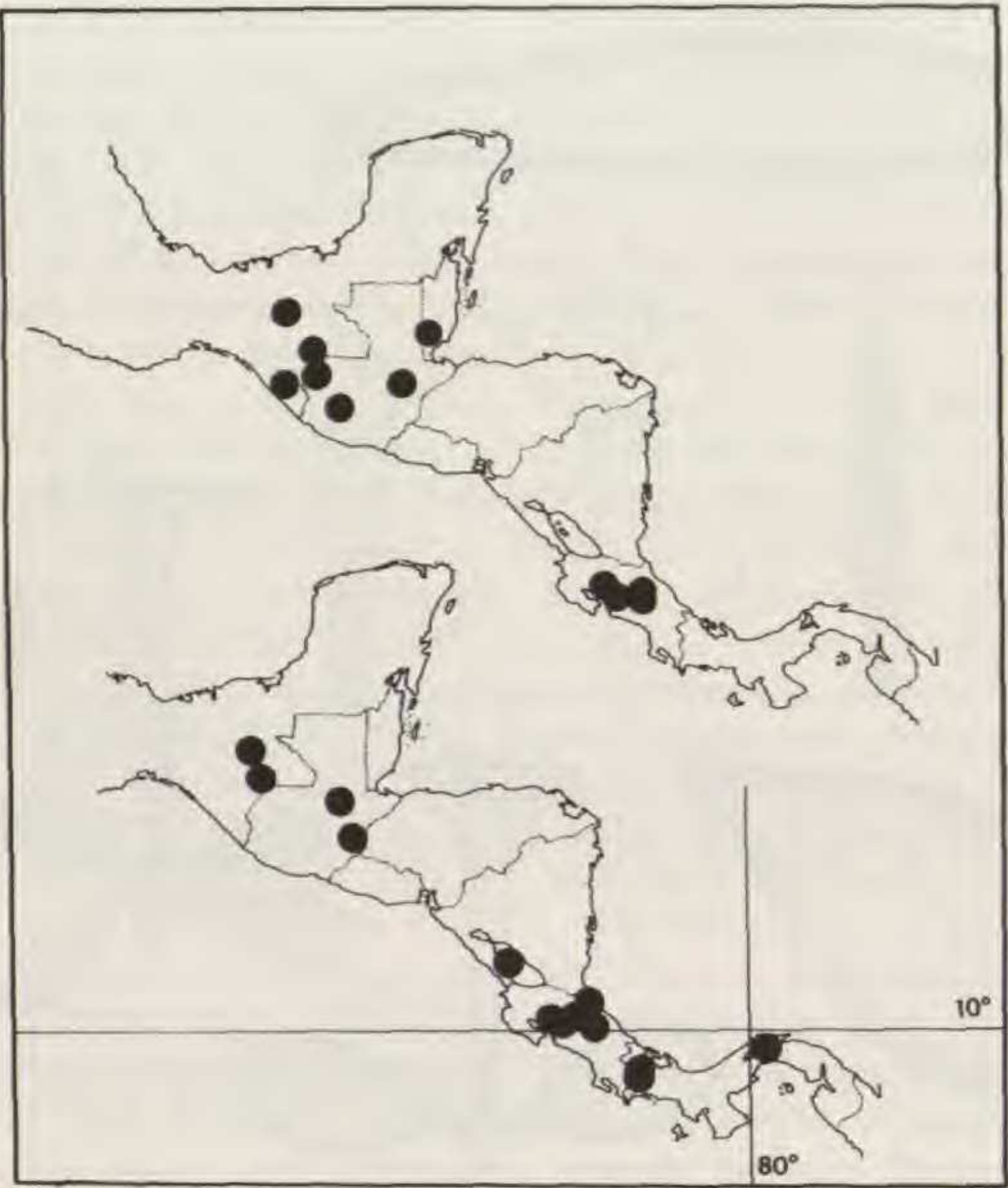


FIGURE 12. Distribution of *Hillia loranthoides* Standl. (upper map) and *H. panamensis* Standl. (lower map) in southern Mexico and Central America.

Representative specimens examined. COSTA RICA. **Alajuela:** La Palma de San Ramón, Brenes 3839 (CR, F), 3847 (CR, F), 5439 (CR, F, NY), 6137 (CR, F), Lent 1692 (CR, F). **Cartago:** El Retiro, Santa Cruz de Turrialba, Valerio 1359 (CR). **Puntarenas:** San Luis River valley 1.5 km upstream from San Luis village, Haber & Hammel 1787 (CR, MO). GUATEMALA. **Baja Verapaz:** Sierra de las Minas ca. 5 km S of Purulha, 1600 m, Williams et al. 41950 (F). **Huehuetenango:** km 332 of the Panamerican Hwy. 5 km E of the Mexican border at La Mesilla, Iltis & Lind G202 (WIS). **Quezaltenango:** Quezaltenango, 2666 m, Vaught 305 (US). MEXICO. **Chiapas:** municipio La Trinitaria, 10 km ENE of Dos Lagos above Santa Elena, 1170 m, Breedlove & Almeda 57488 (CAS, NY). **Oaxaca:** vicinity of Concordia, Montecristo, 1100 m, Makrinus 727 (US).

9. *Hillia tetrandra* Swartz, Prodr. 58. 1788.
TYPE: Jamaica. Coldspring, O. Swartz s.n. (holotype, S not seen; isotype, BM not seen, photo NY).

Hillia tuxtlensis Sessé & Mociño ex DC., Prodr. 4: 351. 1830, nom. inval., pro syn.

Suffrutescent herbs or shrubs to 4 m tall; bark gray-brown, smooth. Leaf blades obovate to elliptic, 3–7.5(–10) cm long, 1–3(–4.5) cm wide, obtuse to usually rounded at apex, attenuate at base, subcoriaceous to coriaceous; secondary veins pinnate,

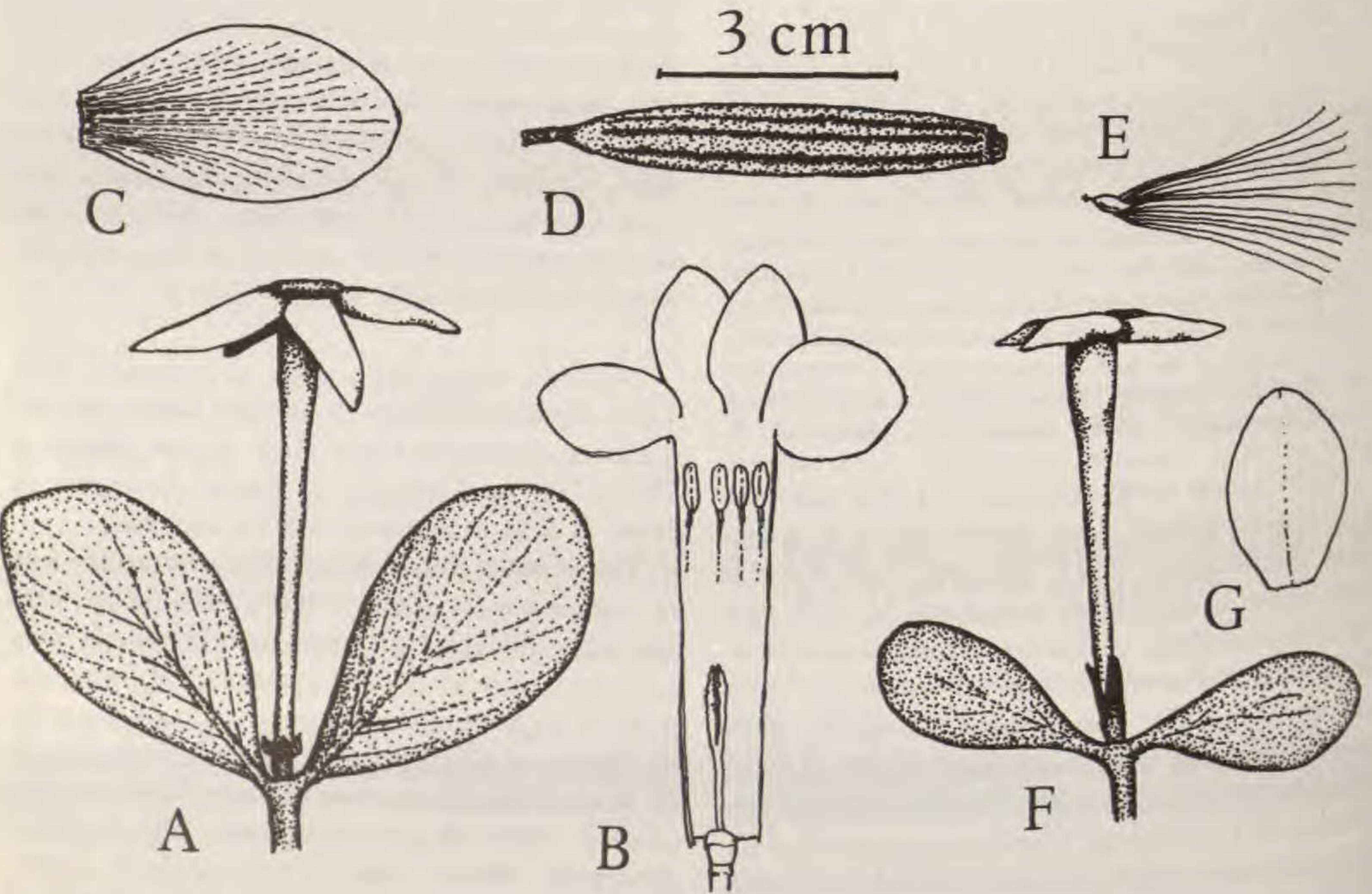


FIGURE 13. A–E. *Hillia tetrandra* Sw.—A. Habit with flower.—B. Flower opened.—C. Stipule (floral).—D. Capsule.—E. Seed. F, G. *Hillia maxonii* Standl.—F. Habit with flower.—G. Stipule (floral). A, B, from Chazaro 3380 (F); C, D, E, from Menéndez L. 85 (F); F, G, from Maxon et al. 7501 (US). A–D, F to same scale, E to three times this scale, G to twice the first scale.

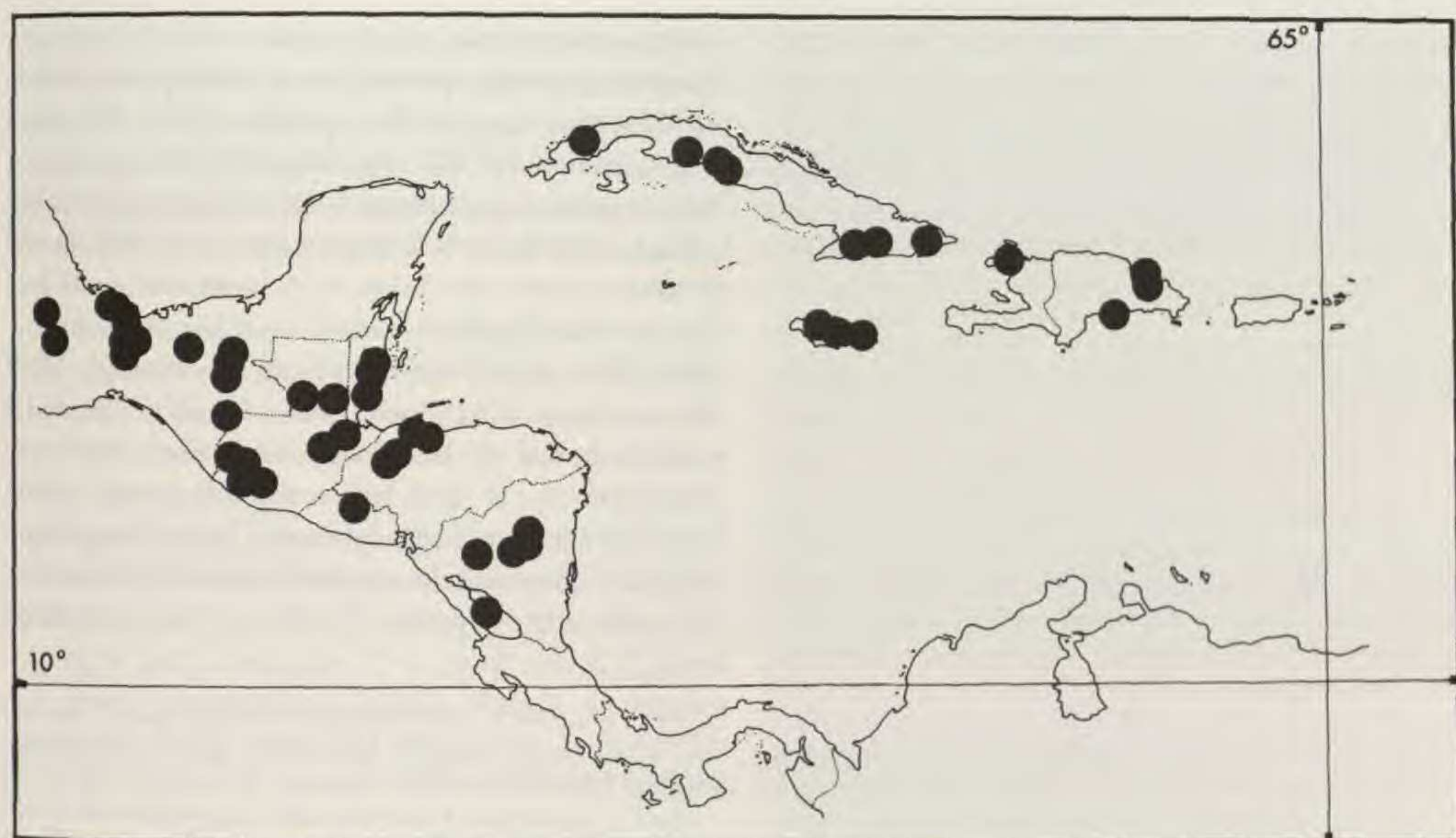


FIGURE 14. Distribution of *Hillia tetrandra* Sw. in southern Mexico, Central America, and the Greater Antilles.

3-5(-6) pairs, plane, without domatia; margins flat; petioles 1-11 mm long; stipules 8-30 mm long, 5-20 mm wide. Flowers solitary; peduncles 1-5(-10) mm long; bracts lacking or 3-4 × 1-2 mm; pedicels 0-3 mm long; calyx limb lacking or divided to base, the lobes 4, 7-19 mm long, often unequal, 1-3(-5) mm wide, oblanceolate to ligulate, rounded; corollas salverform, white, the tube 25-78 mm long, the lobes 4, 10-27 mm long, 8-22 mm wide, elliptic to broadly elliptic, broadly rounded; anthers 4, subsessile, 4.5-5 mm long, with tips positioned 2-3 mm below top of corolla tube; ovary 5-10 mm long; styles 8-18 mm long; stigmas 7-11 mm long, 2-3 mm wide, flattened, linear, positioned below middle of corolla tube. Capsules 25-80 mm long including a beak 1-3 mm long, 5-9 mm diam., not stipitate, with ca. 8 rounded to winged longitudinal ridges to 1 mm high; seeds 2.5-3.5 × 1-1.5 mm, with filaments 8-17 mm long. Figure 13A-E; Standley & Williams (1975: fig. 14).

Habitat, phenology, and distribution (Fig. 14). Cuba, Jamaica, Hispaniola, and southern Mexico to northern Nicaragua, in moist to wet, usually rocky forests at 0-1350(-2650) m. Collected in flower March to November, in fruit throughout the year.

This frequently collected species is characterized by its rounded, usually subcoriaceous leaf blades and ridged capsules. Leaf size in plants from Belize and Honduras is frequently markedly larger than

in plants from other areas. Some individual plants from Guatemala, Belize, and Mexico lack a calyx limb; there is no intermediate stage with reduced lobes. This sporadic absence of a calyx limb is found in other *Hillia* species and does not appear to be of taxonomic significance. The corollas vary by as much as 100% in size on material studied, although this may be largely due to shrinkage in dried specimens.

Hillia tetrandra is similar to *H. maxonii* of southern Nicaragua to Colombia. The latter can be separated by its smooth to only very slightly ridged capsules and thickly coriaceous leaf blades with the secondary veins usually not discernible. Specimens that lack capsules may be difficult to separate, particularly in Nicaragua where the species occur together. These two species appear to differ ecologically: plants of *H. tetrandra* are generally found below 1000 m in moist formations, while *H. maxonii* is usually reported from very wet forests on ridgetops above 800 m, or from coastal mangrove formations.

Representative specimens examined. BELIZE. **El Cayo:** Mt. Pine Ridge, banks of Río On, Lundell 6799 (F, GH, NY, US). **Stann Creek:** Middlesex, Gentle 3006 (MO, NY). **Toledo:** Río Grande, Schipp S-585 (A, F, GH, MO, NY). CUBA. **Cienfuegos:** Buenos Aires, Roig & Acuña 6104 (NY). **Granma:** Pico Turquino, Loma Cordero, Bucher 47 (NY). **Guantánamo:** near Laguna del Galano, Toa, Alain 3856 (GH). **Las Villas:** Trinidad Mountains, near El Naranjo, Webster et al. 209 (A). **Pinar del Río:** Rangel, Rosario Mountains, Alain 6034 (GH, NY). **Santiago de Cuba:** Gran Piedra, Clemente 7144 (GH, US). **Villa Clara:** Las Lagunas, Buenos Aires,

Jack 6812 (A, DS, F, NY). DOMINICAN REPUBLIC. **El Seibo:** Parque Nacional Los Haitises, entre la caseta #1, Cueva de Arena, y Boca de Infierno, 19°05'N, 69°27'30"W, *Zanoni et al. 35961* (NY). **Samaná:** Samaná Peninsula, Laguna, N of Pan de Azúcar, *Ekman 15099* (GH, US). **San Cristóbal:** near El Cacao, 500 m, *Liogier 17770* (F, NY). EL SALVADOR. **Santa Ana:** Finca Pilón on Cerro de los Naranjos, Volcán Santa Ana, *Williams et al. 15135* (F). GUATEMALA. **Alta Verapaz:** Cubilquitz, *von Tuerckheim 7920* (GH, NY, US). **Izabal:** Río Dulce between Livingston and 6 mi. upriver on N side, *Steyermark 39464* (A, F). **Petén:** La Cumbre, 5 km E on Pusila River bank, *Contreras 8873* (CAS, MO), *8893* (CAS, MO). **Quezaltenango:** Río Samala near Santa María de Jesús, *Standley 84616* (F). **San Marcos:** 6 mi. SW of Tajumulco, NW slopes of Volcán Tajumulco, *Steyermark 36731* (F, NY). **Sololá:** woods bordering Río Bravo in the vicinity of Finca Moca, S-facing slopes of Volcán Atitlán, *Steyermark 479564* (F, US). **Suchitepequez:** S-facing slopes of Volcán Santa Clara 1.5–2 mi. W of Finca El Naranjo, *Steyermark 46808* (F). HAITI. **Nord:** Massif du Nord, sobre Morne Bonnet Levêque, al SO de Milot, 19°6'N, 72°14'W, *Mejía 35780* (NY). HONDURAS. **Atlántida:** Lancetilla Valley near Tela, *Standley 52736* (A, F, US), *54583* (A, F, US), *55581* (A, F, US). **Cortes:** Santa Cruz de Yojoa, *Edwards 654* (A, US). **Santa Bárbara:** near Mochito, *Dickson 1352* (US). JAMAICA. **Cornwall:** Trelawney, Tyre near Troy, *Harris 9448* (F, NY, US). **Middlesex:** St. Catherine, Mt. Diablo, site of Blue Mountain, 2.5 mi. S by road of Hollymount Road, *Hespenheide et al. 1389* (DUKE, GH). **Surrey:** St. Thomas, trail from Bath to Corn Puss Gap, just S of the gap, *Anderson & Sternberg 3311* (DUKE, GH, US). MEXICO. **Chiapas:** mpio. Ocosingo, 5 km SW of Santo Domingo, 120 km SE of Palenque on road to Bonampak, *Davidse et al. 20416* (MO). **Oaxaca:** road between Ixtlán & Valle Nacional, 13 mi. by road above Valle Nacional, 17°40'N, 96°22'W, *Webster & Breckon 15378* (MO). **Tabasco:** mpio. Teapa, Puyacatengo, *Ventura 20644* (F, MO). **Veraacruz:** municipio San Andrés Tuxtla, Los Tuxtlas biological station, 18°34'–36'N, 95°04'–09'S, *Ibarra 202* (MO), *547* (NY), *1025* (NY), *1983* (MO), *1984* (MO), *Martínez 3075* (F, MO, US). NICARAGUA. **Matagalpa:** Los Tres Laureles, *Neill 7259* (MO). **Rivas:** Isla Ometepe, Volcán Concepción, Altagracia "La Sabana," 11°32'N, 85°35'W, *Robleto 138* (MO). **Zelaya:** Cerro Waylawas, 13°39'N, 84°48'–49'W, *Stevens 7404* (MO).

- 10. *Hillia maxonii*** Standley, J. Wash. Acad. Sci. 18: 163. 1928. TYPE: Nicaragua. Managua: Las Nubes and vicinity S of Managua, 800–900 m, 28 June 1928, *W. R. Maxon, A. D. Harvey & A. T. Valentine 7501* (holotype, US, photo F).

Cosmibuena rhizophorae Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 178. 1940. TYPE: Colombia. Valle: Buenaventura Bay, 0 m, 13 Apr. 1939, *E. P. Killip 34972* (holotype, US, photo F; isotype, F).

Suffrutescent herbs or shrubs to 5(–15) m tall; bark gray-brown, smooth. Leaf blades elliptic to oblanceolate or suborbicular 2.5–10 cm long, 15–35 mm wide, obtuse to rounded at apex, cuneate

to attenuate at base, coriaceous to usually thickly so; secondary veins pinnate, 4–5 pairs, plane, without domatia; margins flat; petioles 3–8(–15) mm long; stipules 12–32 mm long, 8–10 mm wide. Flowers solitary; peduncles 1–2(–4) mm long; bracts lacking or 1–3 × 1–2 mm; calyx limb lacking or divided to base, the lobes 4, 5–6 mm long, 0.5–2 mm wide, ligulate, acute; corollas salverform, white, the tube 42–55 mm long, the lobes 4, 15–27 mm long, 10–17 mm wide, elliptic, rounded; anthers 4, ca. 5 mm long, subsessile, with tips positioned ca. 3 mm below top of corolla tube; ovary 3–10 mm long; style ca. 15 mm long; stigmas ca. 7 mm long, linear, positioned below middle of corolla tube. Capsules 29–60 mm long including beak 1–3 mm long, 5–9 mm diam., not stipitate, smooth to slightly ridged longitudinally; seeds 2–4 × 0.5–1 mm, with filaments 6–13 mm long. Figure 13F, G.

Habitat, phenology, and distribution (Fig. 15). Central Nicaragua to Ecuador, in wet forests at 0–2400 m: montane regions, Nicaragua to Panama, to mangrove formations and along rivers, Panama to Ecuador. Collected in flower April, May, July to September, and December, in fruit January to March, May to July, November, and December.

This species is characterized by its coriaceous leaf blades that are obtuse to rounded at the apex and smooth to slightly ridged capsules. Plants from Colombia and Ecuador are apparently disjunct by several hundred miles from those of central Pan-



FIGURE 15. Distribution of *Hillia illustris* (Vell.) K. Schum. (solid circles) and *H. maxonii* Standl. (solid triangles) in Central and South America.

ama and are found in coastal formations rather than wet ridge forests. In Panama plants have been collected in both habitats. No morphological differences between the Central and South American plants are evident. *Cosmibuena macrocarpa* (Benth.) Walp. occupies a similar geographic range and set of habitats.

Hillia maxonii is similar to *H. tetrandra*, and these species have sometimes been combined (Dwyer, 1980). The distinctions between them are discussed under the treatment of the latter species. *Hillia maxonii* is also similar to *H. palmana* of southern Central America; this latter species has consistently smaller flowers and usually smaller leaves.

Representative specimens examined. COLOMBIA. **Chocó-Valle Border Region:** Alto del Galápago, along Ansermanuevo-San José del Palmar road, 4°40'N, 76°25'W, Luteyn & Giraldo 12690 (CUVC). **Valle:** Estero del Cangrejal, entre los ríos Yurumanguí y Naya, Cuatrecasas 16017 (F, US). COSTA RICA. **Alajuela:** La Palma de San Ramón, Brenes 11900 (F, NY). **Cartago:** near La Sierra ca. 25 km S of Cartago, Williams et al. 28129 (F). **Guanacaste:** El Silencio near Tilarán, Standley & Valerio 44733 (US). **Heredia:** Cerros de Zurquí NE of San Isidro, Standley & Valerio 50691 (US). **Puntarenas:** Monteverde Reserve, Haber 571 (MO), 1787 (MO), 4501 (MO), Hammel & Haber 13933 (MO). **San José:** near Finca La Cima above Los Lotes, N of El Copey, Standley 42599 (US), 42771 (US). ECUADOR. **Carchi:** environs of Chical 12 km below Maldonado on Río San Juan, 1°04'N, 78°17'W, Madison et al. 4700 (F). NICARAGUA. **Managua:** S of Managua, Garnier 135 (F). PANAMA. **Bocas del Toro:** near Cerro Colorado ca. 9.4 mi. from Chami camp, 8°35'N, 81°45'W, McPherson 8941 (MO). **Chiriquí:** distrito Boquete, Fortuna Dam site, van der Werff & van Hardeveld 6722 (MO). **Coclé:** western slopes and summit of Cerro Valle Chiquito, Seibert 495 (MO, US). **Panamá:** Cerro Jefe (Cerro Azul), 9°15'N, 79°23'W, Dwyer & Gauger 7377 (GH, MO), McPherson 6858 (MO), 7138 (MO), Mori & Kallunki 6500 (MO, NY). **Veraguas:** 5 mi. W of Santa Fe on road past Escuela Agrícola Alto Piedras, Croat 23079 (F, MO, NY).

11. *Hillia palmana* Standley, J. Wash. Acad. Sci. 18: 164. 1928. TYPE: Costa Rica. Heredia: vicinity of La Palma on road to La Hondura 1500–1700 m, 17–18 July 1923, W. R. Maxon & A. D. Harvey 8045 (holotype, US).

Hillia chiapensis subsp. *grandifolia* Dwyer, Ann. Missouri Bot. Gard. 67: 216. 1980. TYPE: Panama. Veraguas: 6–7 km W of Santa Fe on new road past agriculture school, 2900 ft. [950 m], M. Nee 9698 (holotype, MO).

Suffrutescent herbs or shrubs to 5 m tall; bark gray-brown, smooth. Leaf blades elliptic to oblanceolate, 2–7 cm long, 1.5–3.5 cm wide, obtuse to

rounded or rarely truncate at apex, cuneate to attenuate at base, coriaceous; secondary veins pinnate, 3–4 pairs, plane, without domatia; margins flat; petioles 3–8 mm long; stipules 12–20 mm long, 8–10 mm wide. Flowers solitary; peduncles 1–2 mm long; bracts lacking or 1–3 × 1–2 mm; calyx limb lacking or divided to base, the lobes 4, 4–6 mm long, 1–2 mm wide, ligulate, acute to rounded; corollas salverform, white, the tube 35–40 mm long, the lobes 4, 8–12 mm long, 6–12 mm wide, elliptic to suborbicular, rounded; anthers 4, ca. 5 mm long, subsessile, with tips positioned 2–3 mm below top of corolla tube; ovary 3–5 mm long; style ca. 15 mm long; stigmas ca. 7 mm long, linear, positioned below middle of corolla tube. Capsules 3–6 cm long including beak 1–3 mm long, 5–8 mm diam., not stipitate, smooth; seeds 2–4 × 0.5–1 mm, with filaments 6–13 mm long. Figure 11D, E.

Habitat, phenology, and distribution (Fig. 16). Central Nicaragua to central Panama, in wet forests at 675–2500 m. Collected in flower December to October, most frequently May to June, in fruit December to February, May, and July to October.

This species is distinguished by its medium-sized leaf blades that are usually obtuse to rounded at the apex and small flowers. It is similar to *Hillia maxonii* and *H. panamensis*; the distinctions among these three species are discussed in the treatments of the last two species.

Representative specimens examined. COSTA RICA. **Alajuela:** Fila Volcán Viejo, San Carlos, Gómez-Laurito 11095 (CR). **Cartago:** Volcán Irazú, SW slopes near Guayabillos, Cufodontis 465 (F). **Guanacaste:** entre la laguna del Arenal y el Alto de La Carpintera, cerca de Tilarán, Brenes 12644 (F, NY). **Heredia:** entre Finca La Georgina y Vara Blanca, Jiménez 2075 (CR, F, NY). **Limón:** Reserva Indígena Talamanca, camino a Soki entre la quebrada Amubri, margen izquierda del río Lari, 9°29'40"N, 82°03'40"W, 200 m, Chacón 18 (MO). **Puntarenas:** Monteverde area, 10°20'N, 84°50'W, W. Haber 760 (MO), 1156 (MO), 4564 (MO), 6174 (MO), Haber & Bello 3671 (CR, MO), 4263 (CAS, CR, MO), 4267 (CR, MO), 4530 (MO). **San José:** near Altos de Tablazo ca. 7 km SSE of Higuito, ca. 9 km SSE of Desemparados, Wilbur 19782 (CAS, CR, F, MO, NY, US). NICARAGUA. **Boaco:** 2 km al N de San José de los Remates, 12°36'N, 85°45'W, Moreno 24904 (MO), 24936 (MO). **Granada:** lado NO del volcán Mombacho, Finca San Joaquín, 11°50'N, 85°59'W, Moreno & Henrick 8510 (MO). **Jinotega:** ca. 1.5 km from Hwy. 3 on road to Aranjuez, 13°02'N, 85°55'W, Stevens 5947 (MO). **Matagalpa:** ridge along road between La Danta and La Luna, 12°40'N, 85°43'W, Stevens 9616 (MO). PANAMA. **Bocas del Toro:** trail from Boquete to Cerro Pate Macho, 8°49'N, 82°24'W, McPherson & Merello 8328 (MO). **Chiriquí:** vicinity of Fortuna Dam, 8°40'N, 79°50'W, McPherson 10577 (MO). **Darién:** E slope of

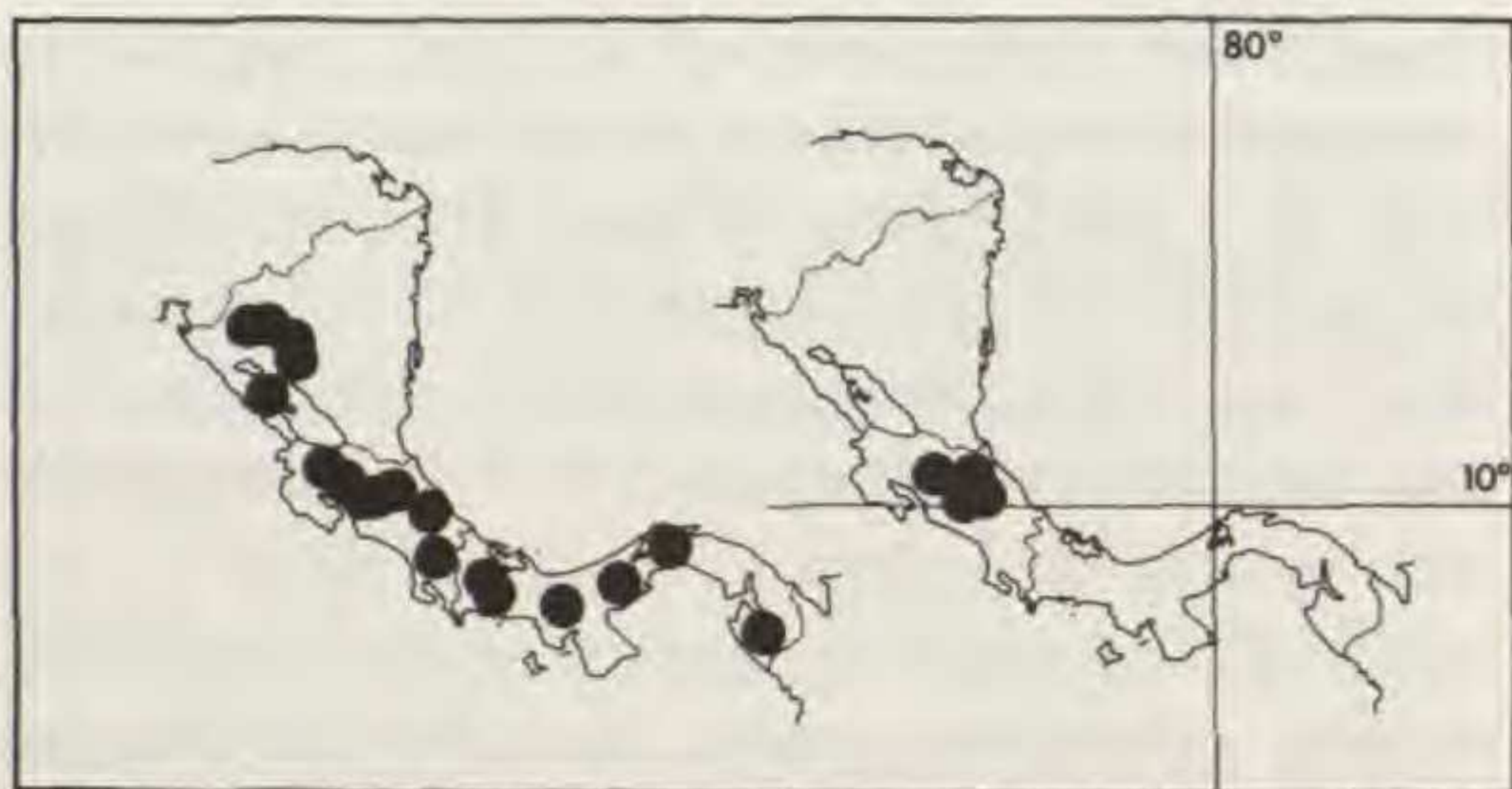


FIGURE 16. Distribution of *Hillia palmana* Standl. (left-hand map) and *H. grayumii* C. M. Taylor (right-hand map) in Central America.

Cerro Sapo, Hammel 1284 (MO). **Panamá:** E slope of Cerro Jefe (Cerro Azul), Tyson 3436 (GH, MO). **Vera-guas:** Cerro Tute, 8°32'N, 81°07'W, Knapp & Dressler 5398 (MO), Mori et al. 7559 (MO).

12. *Hillia panamensis* Standley, N. Amer. Fl. 32(2): 117. 1921. TYPE: Panama. Chiriquí: Cerro de la Horqueta around Los Sigüas Camp, 1700 m, 17–19 Mar. 1911, H. Pittier 3190 (holotype, US; isotype, US).

Hillia chiapensis Standl., J. Wash. Acad. Sci. 16: 16. 1926. TYPE: Mexico. Chiapas: near Fénix, Apr. 1925, C. A. Purpus 262 (holotype, US, photo F).

Hillia hathewayi Fosberg, Sida 2: 387. 1966. TYPE: Costa Rica. Heredia: S slope of Volcán Barba, 1950 m, 26 May 1965, W. H. Hatheway 1371 (holotype, US; isotypes, F, GH).

Suffrutescent herbs or shrubs to 4 m tall; bark gray-brown, smooth. Leaf blades elliptic to narrowly elliptic, 6–15 mm long, 3–10 mm wide, rounded to obtuse at apex, cuneate to attenuate at base, subcoriaceous to coriaceous; secondary veins pinnate, ca. 2 pairs, smooth, without domatia; margins flat; petioles 1–2 mm long; stipules 4–5 mm long, 1–1.5 mm wide. Flowers solitary; peduncles ca. 1 mm long; bracts lacking; calyx limb usually lacking or divided to base, the lobes 4, 6–7 mm long, 1–3 mm wide, ligulate, rounded; corollas white, salverform, the tube 24–35 mm long, the lobes 4, 8–10 mm long, 3–5 mm wide, lanceolate, acute; anthers 4, 1–2 mm long, subsessile, with tips positioned 1–2 mm below top of corolla tube; ovary 2–3 mm long; style 7–12 mm long; stigmas 5–10 mm long, linear, positioned below middle of corolla tube. Capsules 2–4 cm long including beak 1–2 mm long, ca. 3 mm diam., not stipitate, smooth or usually with ca. 10 longitudinal ridges; seeds 1–2 × 0.5 mm, with filaments 6–13 mm long. Figure 11F–I; Dwyer (1980: fig. 48, as *Hillia chiriquiensis*).

Habitat, phenology, and distribution (Fig. 12). Southern Mexico to Guatemala and Belize,

and southern Nicaragua to western Panama, in wet forests at 20–2300 m. Collected in flower December, January, and June through August, in fruit November to April, August, and September.

This species is distinguished by its lanceolate acute corolla lobes and relatively small, usually narrow leaf blades, stipules, and capsules. The plants of southern Mexico and Guatemala are apparently disjunct from those of southern Central America, but no morphological differences are apparent and they appear to occupy similar habitats. Therefore *Hillia chiapensis* is here placed in synonymy. Similar apparently disjunct geographic ranges are seen in *H. loranthoides* and species of *Psychotria* (Hamilton, 1989).

Hillia panamensis is similar to *H. palmana*; the latter species has elliptic rounded corolla lobes 6–12 mm wide, and usually larger, proportionally broader leaf blades, stipules, and capsules.

Several sterile and fruiting specimens from relatively low elevations in Nicaragua and Costa Rica are provisionally included here, although they have relatively broad leaves and ridged capsules.

Representative specimens examined. BELIZE. **Toledo:** Maya Mountains, Holst 4292 (MO). COSTA RICA. **Alajuela:** Cantón Alfaro Ruiz, Palmira, Smith 2737 (F). **Cartago:** Turrialba, Instituto Interamericano de Ciencias Agrícolas, León 2999 (CR). **Guanacaste:** El Dos de Tilarán, 13 km NW of Monteverde, 10°25'N, 84°55'W, 900 m, Haber et al. 5273 (MO). **Limón:** Cerro Coronel, E of Laguna Danto, 10°41'N, 83°38'W, Stevens 23919 (CR), Stevens & Montiel 24389 (CR, MO). **Puntarenas:** Monteverde area, Haber 384 (MO), 562 (MO). GUA-TEMALA. **Alta Verapaz:** between Finca Chimote near Rubeltien and Finca Cubilgüitz, Steyermark 44195 (F, US). **Chiquimula:** Cerro Tixixí 3–5 mi. N of Jicotán, Steyermark 31627 (F, NY). MEXICO. **Chiapas:** municipio de Ocosingo, near Laguna Ocotal Grande ca. 25–30 km SE of Monte Líbano, ca. 45 km E of Ocosingo, Dressler 1487 (NY, US). NICARAGUA. **Rivas:** Isla de Ometepe, Volcán Maderas, 11°26–37'N, 85°30–33'W, Moreno 18806 (MO), 19689 (MO), 19852 (MO), Stevens 6552 (MO). PANAMA. **Bocas del Toro–Chiriquí Border:** Cerro Colorado, 8 km from intersection of the ridge road on the road to Escopeta, Folsom 4785 (MO). **Panamá:** Cerro Jefe, Hayden 1021 (MO).

4. *Hillia* subg. *Illustres* C. M. Taylor, sub-nov. TYPE: *Hillia illustris* (Vell.) K. Schum.

A subgeneribus ceteris *Hilliae* corollis infundibularibus 5–9-lobatis viridibus flavovirentibus vel colore atropurpureo suffusis et stigmatibus subcapitatis supra antheras positus differt.

Calyx limb lacking, very reduced, or with 5–9 well-developed lobes; *corollas* membranaceous to carnose, funnellform, green to yellow-green or flushed with dull dark purple, the lobes 5–9, triangular to suborbicular; *stamens* attached above middle or near top of corolla tube, the anthers

subsessile or with filaments well developed; *stigmas* subcapitate, positioned above anthers; *capsules* usually stipitate.

Seven species throughout northern and central South America, one extending north to Costa Rica.

13. *Hillia grayumii* C. M. Taylor, Selbyana 12: 137. 1991. TYPE: Costa Rica. Heredia: Finca La Selva, the OTS field station near Puerto Viejo de Sarapiquí, near the junction of the Ríos Puerto Viejo and Sarapiquí, 100 m, 5 May 1980, M. H. Grayum 2793 (holotype, DUKE; isotype, DUKE).

Shrubs to 1 m tall, or lianas; bark gray-brown, smooth. Leaf blades elliptic, 9–16 cm long, 1.5–6.5 cm wide, acuminate at apex with tip 1–2 cm long, acute at base, coriaceous; secondary veins pinnate, 3–6 pairs, plane, without domatia; margins flat; petioles 3–20 mm long; stipules ca. 4 cm long, 6–8 mm wide. Flowers solitary; peduncles 2–3 mm long; bracts 1–2 mm long; pedicels 2–3(–5) mm long; calyx limb ca. 0.5 mm long, truncate to dentate; corolla broadly funnelform, bright pale green to yellow-green, the tube 43–50 mm long, the lobes 6, 8–9 mm long, triangular, obtuse to rounded; stamens 6, the filaments ca. 10 mm long, the anthers ca. 9 mm long, with tips positioned 3–5 mm below top of corolla tube; ovary 7–8 mm long; stigmas ca. 3 mm long, subcapitate, positioned immediately above anthers. Capsules ca. 12 cm long, ca. 12 mm diam., not stipitate, smooth or with 8–10 low longitudinal ridges; seeds ca. 3 × 0.5 mm, with filaments 15–16 mm long. Taylor et al. (1991: fig. 3).

Habitat, phenology, and distribution (Fig. 16). Costa Rica, in wet forest at 0–200 m. Collected in flower May and June, in fruit March.

This species is distinguished by its reduced calyx limb and bright pale green to yellow-green, broadly funnelform corollas. It is similar to *Hillia illustris* and *H. psammophila* of South America; the distinctions among these are discussed in the treatments of the other two species. Vegetatively *H. grayumii* resembles *H. triflora* var. *triflora*, with which it is sympatric, and these species can be difficult to separate in fruit.

Hillia grayumii appears to be uncommon and ephemeral. It was first discovered in a well-studied area of the La Selva Biological Station, where it apparently grew to flowering size rapidly, but within two years was no longer found in the vicinity (Hammel, pers. comm.; Grayum, pers. comm.).

Representative specimens examined. COSTA RICA. **Alajuela:** Monteverde Biological Reserve, Río Peñas

Blancas, 10°19'N, 84°43'W, Haber & Cruz 8464 (CR). **Cartago:** on Casa de Tajas ridge above Río Gato, 9°47'N, 83°41'W, Lent 3703 (F, NY). **Limón:** shores of Caño Pereira, 10°45–47'N, 83°36–37'W, Stevens et al. 25120 (CR, MO).

14. *Hillia psammophila* Steyermark, Mem. New York Bot. Gard. 19(5): 211. 1963. TYPE: Venezuela. Bolívar: vecinidad del Camp 125 en el Km 125, entre Luepa y Cerro Venamo, vecinidad de Cerro Uei, 1100 m, 20 Apr. 1960, J. Steyermark & S. Nilsson 392 (holotype, VEN).

Suffrutescent vines, climbing by adventitious roots; bark smooth. Leaf blades elliptic to lance-elliptic, 4.5–6.5 cm long, 2–3 cm wide, acuminate at apex with tip 4–10 mm long, acute at base, coriaceous; secondary veins pinnate, 3–4 pairs, plane, without domatia; margins flat; petioles 6–11 mm long; stipules not seen. Flowers solitary; peduncles 4–5 mm long; bracts not seen; calyx limb divided to base, the lobes 6, ca. 18 mm long, 3–3.5 mm wide, triangular to narrowly elliptic, rounded; corollas funnelform, yellow-green, the tube ca. 6 cm long, the lobes 6, ca. 1 cm long, ca. 15 mm wide, rounded; anthers 6, sessile, 7–8 mm long, with tips positioned ca. 5 mm below top of corolla tube; ovary ca. 7 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules not seen. Steyermark (1963: fig. 74).

Habitat, phenology, and distribution (Fig. 8). South-central Venezuela, in wet forests at 1100 m. Collected in flower in April.

This species is distinguished by its relatively small leaves and anthers situated just below the top of the corolla tube. The original and subsequent descriptions of this species (Steyermark, 1963, 1974) describe the filaments as ca. 15 mm long, but the anthers are sessile and the filaments adnate to the corolla for ca. 45 mm. *Hillia psammophila* is similar to *H. illustris*; the distinctions between them are discussed in the treatment of the latter species. *Hillia psammophila* is also similar to *H. grayumii* of Costa Rica and may be closely related; *H. grayumii* differs in its larger leaf blades, 9–16 cm long, and its anthers positioned just below the top of the corolla tube.

15. *Hillia illustris* (Vellozo) K. Schumann in Martius, Fl. Bras. 6(6): 202. 1889. *Saldanha illustris* Vell., Fl. Flum. 3: 141, t. 157. 1825. TYPE: Brazil. Rio de Janeiro area, Vell., Fl. Flum. t. 157, 1825, lectotype designated by Taylor (1993).

Hillia tubaeiflora Cham., Linnaea 9: 260. 1834. TYPE:

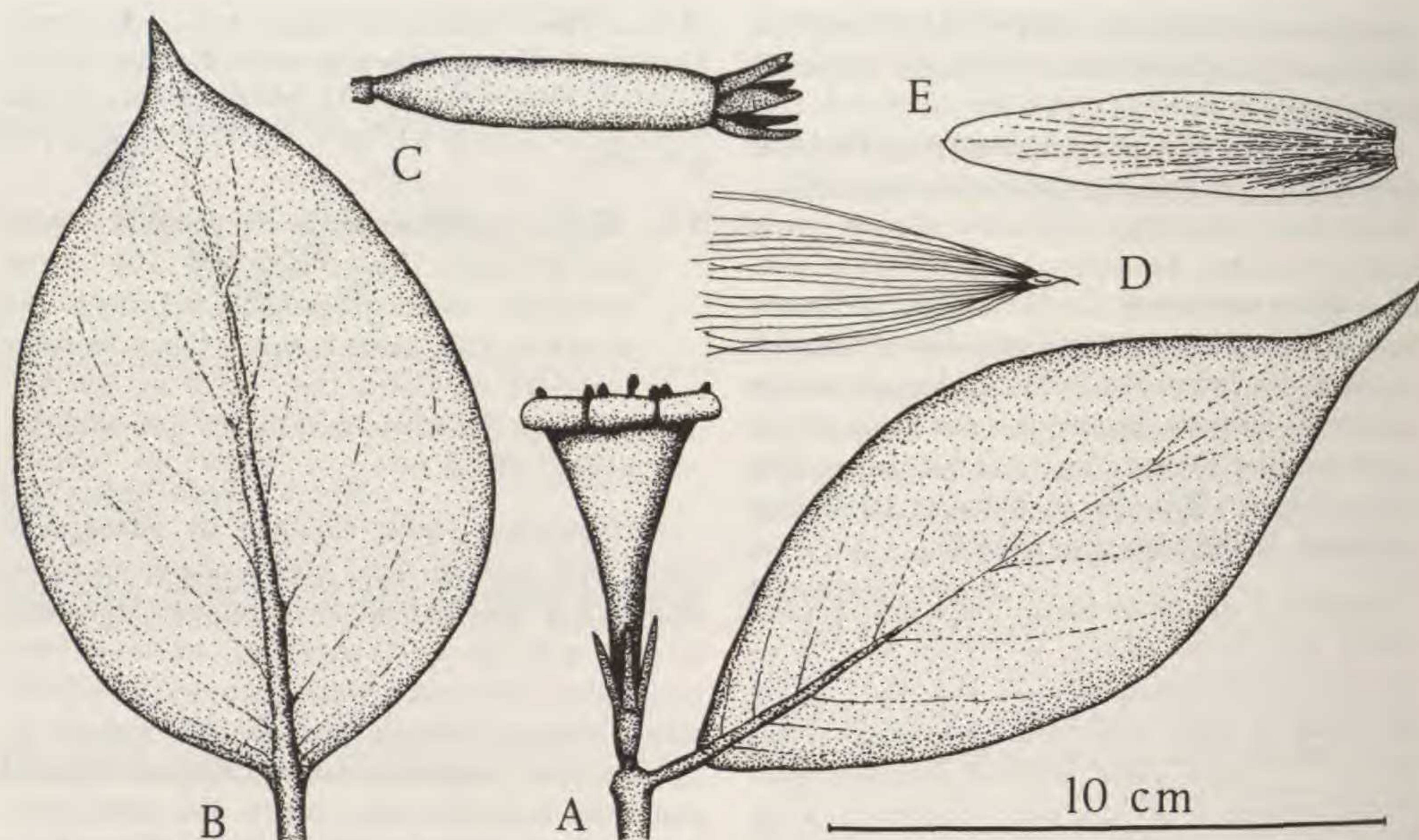


FIGURE 17. A–E. *Hillia illustris* (Vell.) K. Schum. — A. Habit with flower. — B. Leaf. — C. Capsule. — D. Seed. — E. Stipule (floral). A, E, from *Dusén* 15539 (MO); B, from *Vásquez & Jaramillo* 4130 (MO); C, D, from *Encarnación* 26178 (MO). A–C to same scale, D to three times this scale, E to twice the first scale.

Brazil. *Brazilia aequinoctialis*, *Sello* 5988 (holotype, B destroyed, photos F, GH, NY; isotype, F).

Hillia trinitensis R. O. Williams & Cheeseman, *Fl. Trinidad & Tobago* 2: 7. 1928. TYPE: Trinidad. Taruaria Forest, 16 Feb. 1915, *W. E. Broadway* 7807 (lectotype, designated by Steyermark (1972: 288), NY; isotype, TRIN not seen).

Hillia goudotii Standl., *Publ. Field Columbian Mus., Bot. Ser.* 8: 338. 1931. TYPE: Colombia. Valle: Río Sucio, Jan. 1844, *J. Goudot s.n.* (holotype, P, photo F; isotype, F).

Suffrutescent herbs, shrubs, or small trees to 8 m tall; bark gray-brown to red-brown, smooth, sometimes peeling. Leaf blades elliptic, 8.5–15 cm long, 3–8 cm wide, acute to usually acuminate at apex with tip 5–10(–15) mm long, acute to cuneate at base, thickly coriaceous; secondary veins pinnate, 4–7 pairs, plane or with midrib sometimes prominent abaxially, without domatia; margins flat; petioles 6–13 mm long; stipules subtending leaves 23–33 mm long, 7–10 mm wide, those subtending flowers 26–60 mm long, 6–18 mm wide. Flowers solitary(–3); peduncles 1–5 mm long; bracts not seen; calyx limb divided to base, the lobes 6, 9–35 mm long, often unequal by ca. 1 mm, 1.5–2(–4) mm wide, narrowly triangular, acute; corolla funnelform to broadly so, bright green to yellow-green, the tube 48–61 mm long, the lobes 6, 8–16 mm long, elliptic, obtuse to rounded; anthers 6, subsessile, 10–11 mm long, with tips positioned at or 1–2 mm above top of corolla tube;

ovary 6–10 mm long with stipe 1–5 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules with peduncles 2–10 mm long, (50–)85–115 mm long including beak 1–5 mm long, 8–15 mm diam., stipe 5–10 mm long, smooth or usually with ca. 10 low longitudinal ridges; seeds 2–4 × 0.5–2 mm, with filaments 14–22 mm long. Figure 17; Robbrecht (1988: fig. 6b, as *Hillia tubiflora*).

Habitat, phenology, and distribution (Fig. 15). Sporadic throughout tropical South America, in wet forests at 70–800 m, frequently along rivers. Collected in flower December, January, May to July, and September, in fruit January to March and May to November.

This species is distinguished by its relatively large, acute to acuminate leaf blades with pinnate venation and stipitate capsules. Both vegetative and reproductive parts vary rather widely in size, as in several other species of *Hillia*.

Hillia illustris is similar to *H. ulei*; the latter species is distinguished by its usually shorter, proportionally broader leaf blades with subpalmate venation. *Hillia illustris* also resembles *H. grayumii*, which has capsules that are not stipitate, a very reduced calyx limb, and filaments ca. 10 mm long, and *H. psammophila*, which has smaller leaf blades, filaments ca. 15 mm long, and anthers positioned below the top of the corolla tube.

There appears to be no morphological difference between plants of Trinidad and the mainland, and *Hillia trinitensis* is not maintained here. *Hillia goudotii*, based on a single specimen, differs from typical *H. illustris* only in having flowers borne in a cyme of three rather than solitary. A similar variation in flower number is seen in *H. saldanhae*, and the reverse variation, with flowers usually three but rarely one or two, is found in *H. triflora*. Therefore *Hillia goudotii* is not maintained here. Some authors (e.g., Robbrecht, 1988) have corrected the spelling of *H. tubaeflora* (tuba-shaped) to "tubiflora" (tube-shaped), but Chamisso based his description on a flowering specimen, and most likely intended to apply the first, more appropriate epithet.

Representative specimens examined. BOLIVIA.

Beni: provincia Balliva, lower slopes of Serranía Pilón Lajas, 14.3 km N of bridge over Río Quiquibey, 15°19'S, 67°03'W, *Solomon* 13957 (MO). **La Paz:** provincia Yungas Sur, basin of Río Bopi, Asunta near Evenay, *Krukoff* 10697 (A, F, MO, NY). BRAZIL. **Amapá:** região de Río Jarí Monte Dourado, Planalto Amazônia, *Silva* 927 (NY). **Paraná:** Tacarehy, *Dusén* 15539 (F, GH, MO). **São Paulo:** Sete Varras, S entrance to Carlos Botelho State Park, 24°22'S, 46°55'W, *Gentry et al.* 59053 (MO). COLOMBIA. **Amazonas-Vaupés Border:** río Apaporis, entre el río Pacoa y el río Kananari, Soratama, *Schultes & Cabrera* 13030 (F, NY). **Chocó-El Valle Border Region:** carretera Ansermanuevo-San José de Palmar, Alto de Galápagó, *Forero et al.* 2868 (COL). **Vaupés:** Mitú and vicinity, island in Río Vaupés just below Urania, *Zarucchi et al.* 1885 (COL, F, GH). ECUADOR. **Morona-Santiago:** Misión Bomboiza, 3°29'S, 78°34'W, *Holm-Nielsen & Jeppesen* 4202 (AAU). **Napo:** cantón Tena, 10 km O de la estación biológica Jatún Sacha, carretera hacia Tena, 1°03'S, 77°40'W, *Palacios & Iguago* 4433 (MO). FRENCH GUIANA. **Cayenne:** region de la Haute Armontabo (Bas Oyapock), *de Granville* 4362 (COL, P). **Saint Laurent de Maroni:** Rivière Mana, Crique Arouany, *F. Hallé* 622 (P). PERU. **Cuzco:** provincia La Convención, Camp Zero ca. 1 hour walk up Río Mapitunuari from Río Apurimac, Luisiana, *Dudley* 11426 (F). **Huánuco:** provincia Leoncio Prado, distrito Rupa Rupa, al E de Tingo Maria, cerca al cerro Quemado, *Schunke* 10292 (F, MO, NY). **Loreto:** provincia Maynas, distrito Alto Nanay, along trail to Santa Rosa, Santa María de Nanay, *Simpson & Schunke* 806 (COL, F, MO, NY). SURINAM. **Brokopondo:** 2 km S of Affobakka along Sara Creek, Afterwards Lake, *van Donselaar* 2109 (NY). **Marowijne:** ab Moengotapoe ad Grote Zwiebelzwamp, *Lanjouw & Lindeman* 628 (NY). **Nickerie:** Wilhelmina Gebegte, Zuid River 2 km above confluence with Lucie River, 3°10'-20'N, 56°29'-49'W, *Irwin et al.* 55870 (COL, MO, NY). VENEZUELA. **Anzoátegui:** along Río León NE of Bergantín, *Steyermark* 61433 (F). **Bolívar:** summit of W-facing escarpment E of Miamo, Hato de Nuria, Altiplanicie de Nuria, *Steyermark* 88835 (NY). **Delta Amacuro:** departamento Antonio Díaz, Caño Guinquina, *Marciano et al.* 70-2-77 (MO).

16. *Hillia ulei* K. Krause, Verh. Bot. Vereins Prov. Brandenburg 50: 97. 1908; K. Schum. ex Ule, in H. Karst. & Schenck, Vegetationsbilder 2, sub tab. 1-2: 3. 1904, nom. nud. TYPE: Peru. Loreto: prope Yurimaguas, Aug. 1902, *E. Ule* 6305 (holotype, B destroyed, photos F, GH, MO, NY; isotype, F). Steyermark (1972) cited *Ule* 6303 as the type collection, but this seems to be an error.

Hillia viridiflora Kuhl. & Silveira, Arch. Jard. Bot. Rio de Janeiro 4: 370, t. 34. 1925. TYPE: Brazil. Rio de Janeiro: Rio de Janeiro Botanical Garden, Apr. 1920, *Ule* RB-15737 (holotype, RB not seen; isotype, B destroyed, photos F, MO, NY, US).

Hillia irwinii Steyermark, Mem. New York Bot. Gard. 23: 287. 1972. TYPE: Brazil. Amapá: Río Jarí near Cachoeira Macacoara, 0°53'N, 53°21'W, 200 m, 26 Aug. 1961, *H. S. Irwin & W. A. Egler* 46683 (holotype, NY; isotypes, F, GH, NY, US).

Hillia schultesii Steyermark, Mem. New York Bot. Gard. 23: 287. 1972. TYPE: Colombia. Amazonas-Vaupés border: río Apaporis, entre el río Pacoa y el río Kananari, boca del Pacoa, 250 m, 18 July 1951, *R. E. Schultes & Cabrera* 13075 (holotype, US, photo NY).

Suffrutescent herbs or shrubs to 2 m tall; bark gray-brown, smooth. Leaf blades elliptic to broadly elliptic, 2-6.5(-7.5) cm long, 1.3-4 cm wide, acute to usually acuminate at apex with tip 3-5 mm long, rounded to cuneate at base, thickly coriaceous; secondary veins subpalmate, 5-7 pairs, plane or with midrib sometimes prominulous abaxially, without domatia; margins flat; petioles 4-11 mm long; stipules 5-17 mm long, 1.5-8 mm wide. Flowers solitary; peduncles 1.5-2 mm long; bracts lacking or 2-3 × 0.5-1.5 mm; calyx limb divided to base, the lobes 7-10, 8-15 mm long, often unequal by 1-3 mm, 1-2 mm wide, narrowly ligulate to triangular, acute to rounded; corollas broadly funnellform, bright green to yellow-green, the tube 28-39 mm long, lobes 7-10, 6-7 mm long, rounded; anthers 8, subsessile, 6-8 mm long, with tips positioned at top of corolla tube; ovary 5-10 mm long, stipes 8-10 mm long; stigmas ca. 2 mm long, subcapitate, positioned immediately above anthers. Capsules with peduncles 1.5-3 mm long, 6-10.2 cm long including beak 1-5 mm long, 8-10 mm diam., stipes 8-15 mm long, smooth; seeds 1-2 × 0.5-1 mm, with filaments 11-24 mm long. Figure 18.

Habitat, phenology, and distribution (Fig. 6). Sporadic throughout tropical South America and eastern Panama, in wet forests at 0-900 m, most frequently along rivers. Collected in flower March to May, July, and August, in fruit January, March to May, July to September, and November.